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An individual-based model to predict the spatial distribution of northern pike, European perch and pikeperch from habitat use in a reservoir subject to water level fluctuations

Un modèle individu-centré pour prédire la distribution spatiale du brochet, de la perche commune et du sandre, à partir de l'utilisation de l'habitat dans un réservoir soumis à des fluctuations de niveau d'eau

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Abstract – Reservoirs are subject to artificial water level fluctuations leading to a degradation of the littoral habitats. This often results in reduced productivity and biological diversity, particularly for fish. The development of predictive tools of fish population dynamics linked to habitat characteristics can help to optimize management actions such as habitat restoration. We developed a spatially explicit individual-based model, the *3Plake* model, which predicts the spatial distribution of three fish species, northern pike, European perch and pikeperch, over seasons and diel cycles according to their habitat use. The model was calibrated with an accurate description of habitat and high spatial and temporal resolution data of fish movements in a French reservoir. The model calibration is only based on a species-specific coefficient of habitat selectivity. It was chosen to (i) match the observed and simulated traveled hourly and daily distances and (ii) minimize a metric quantifying the distance between observed and simulated density maps. The *3Plake* model correctly simulated the means of traveled distances and the species distributions along the year on the study reservoir. The minimal input required (HSI maps and maximum distance range) allows its easy implementation on other reservoirs and fish species. It could be used to assess the impact of habitat restoration or water level management scenarios on fish distribution.

***Keywords* –** Spatially explicit modeling, fish movement, habitat selection, acoustic telemetry.

Résumé – Les réservoirs sont soumis à des fluctuations artificielles du niveau de l'eau entraînant une dégradation des habitats littoraux. Elles entraînent souvent une réduction de la productivité et de la diversité biologiques, en particulier pour les poissons. Le développement d'outils prédictifs de la dynamique des populations de poissons, liés aux caractéristiques de l'habitat, peut aider à optimiser les actions de gestion telles que les mesures de restauration ou de gestion des niveaux d'eau. Nous avons développé un modèle individu-centré spatialement explicite, le modèle *3Plake*, qui prédit la distribution spatiale de trois espèces de poissons, le brochet, la perche commune et le sandre, au fil des saisons et du cycle diurne en fonction de leur utilisation de l'habitat. Le modèle a été calibré grâce à une description précise de l'habitat et des données à haute résolution spatiale et temporelle des déplacements des poissons dans une retenue française. La calibration du modèle est uniquement basée sur un coefficient de sélectivité de l'habitat spécifique à l'espèce. Ce coefficient a été choisi pour (i) faire correspondre les distances parcourues horaires et journalières observées et simulées et (ii) minimiser une métrique quantifiant la distance entre les cartes de densité observées et simulées. Le modèle *3Plake* a simulé correctement les moyennes des distances parcourues et les distributions des espèces tout au long de l'année sur la retenue d'étude. Le minimum de données d'entrée requises permet d'envisager des transpositions sur d'autres réservoirs et espèces piscicoles. Il pourrait être utilisé pour évaluer l'impact de mesures de restauration de l'habitat ou de scénarios de gestion des niveaux d'eau sur la répartition des poissons.

Mots-clés –Modélisation spatialement explicite, mouvement des poissons, selection de l'habitat, telemetrie acoustique.

1 Introduction

Reservoirs provide numerous services worldwide such as hydropower, water supply (*e.g.*, irrigation, drinking water) or flood protection. With more than 45,000 large dams in the world at the beginning of the 20th century (Hjorth & Bengtsson, 2012), reservoirs need to be considered when managing global biodiversity (Liermann *et al.,* 2012; McAllister *et al.,* 2001; Wu *et al.,* 2019). In reservoirs, and more generally in lentic ecosystems, littoral areas are characterized by a greater diversity of both abiotic and biotic structures than pelagic areas (Prchalová *et al.,* 2009; Prchalová *et al.,* 2008; Zohary & Gasith, 2014; Zohary & Ostrovsky, 2011). These structures constitute complex habitats and even hot spots of biodiversity in lakes (Gasith & Gafny, 1998; Schmieder, 2004), providing a high availability of trophic resources (Pierce *et al.,* 1994). Consequently, in lakes and reservoirs, the achievement of many species life cycle depends on the littoral area.

The anthropogenic uses of reservoirs lead to artificial water level fluctuations (WLF) which are very different from those of natural lakes (Wetzel, 1990). Artificial WLF affect littoral habitat structure by bank erosion (Carmignani & Roy, 2017; Hirsch *et al.,* 2017) and by modification of substrate and macrophytes compositions (Evtimova & Donohue, 2014). They can also temporarily prevent fish from accessing breeding (Hudon *et al.,* 2005) or wintering habitats (Cott *et al.,* 2008) and resting or refuge areas (Kaczka & Miranda, 2014; Logez *et al.,* 2016). Thus, littoral area concentrates a lot of restoration projects to sustain fish fauna by improving habitat, *e.g.*, through revegetation of banks, creation of shallow zones with habitat enhancement or deployment of floating islands (de Moraes *et al.,* 2023; Halleraker et al., 2016; Radinger et al., 2023). Their success often remains uncertain (Vanderbosch & Galatowitsch, 2010), in part because it is dependent on multiple underlying management decisions, environmental conditions and difficulties to conduct such an evaluation. Predictive tools of fish population dynamics are valuable for improving success of restoration projects by testing the effects of different scenario, but they are still sparse (Strayer & Findlay, 2010).

Beyond specific reservoir ecosystems, many studies revealed the key role of habitat in population dynamics. Habitat quality drives the demographic parameters of fish populations, such as fecundity, growing or reproductive success (Farò *et al.,* 2021; Hayes *et al.,* 2009). To seek for an optimized physical habitat quality and availability, habitat is also involved in individual movements (Morales & Ellner, 2002; Nathan *et al.,* 2008; Patterson *et al.,* 2008). Finally, these movements contribute to the spatial distribution of species densities (Blanchard *et al.,* 2021). Then, the modelling of individual fish movements frequently uses habitat quality as a main driver (Hovel & Regan, 2008; Railsback *et al.,* 1999; Van Winkle *et al.,* 1998).

In this study, we applied an individual-based approach to model fish movements in relation to habitat use. The individual approach is appropriate to simulate movements at the same resolution than habitat use (Grimm *et al.,* 2006; Railsback *et al.,* 1999). The main objective was to represent the spatial distribution of fish in a reservoir subject to water level fluctuations which frequently modify available habitats. The second objective was to keep a relatively simple calibration to facilitate future applications to other reservoirs concerned with restoration projects. The developed model, the *3PLake* model, was supported by a high resolution dataset collected during previous studies on northern pike (*Esox Lucius*), European perch (*Perca fluviatilis*) and pikeperch (*Sander lucioperca*), three predatory fish species coexisting in a French reservoir (Roy, 2014; Westrelin *et al.,* 2018). These species, common in European reservoirs (Overton *et al.,* 2015; Skov & Nilsson, 2018), show contrasted habitat preferences. Northern pike are mainly littoral (Chapman & Mackay, 1984; Craig, 2008), European perch are more generalist (Imbrock *et al.,* 2005; Pekcan-Hekim *et al.,* 2005) and pikeperch are rather pelagic (Vehanen & Lahti, 2003). We hypothesized that these species showed different spatial distribution in relation with their habitat use and selectivity.

2 Material and methods

2.1 Study site

The Bariousses hydropower reservoir (45.33°N, 1.49°E) is located on the Vézère River in the western central part of France. The water level (WL) varied between altitudes 507.0 m and 513.5 m during the study from March 2012 to March 2014 (Fig. A.1 Appendix A). At the mean WL (511.5 m), the reservoir area was 0.866 km^2, mean depth 7.1 m and maximum depth 19.4 m.

Based on the Secchi transparency depth, the littoral area of the reservoir was defined as the area connected to the bank with a depth lower than 2.5 m. The littoral area varied from 19.5% at low WL (507.0 m) to 13.3% at high WL (513.5 m) of the total reservoir area. Its habitats tended to become more homogeneous with a lowering structural complexity when the WL dropped: while gravel/pebble, immersed grass and emerging trees dominated at high levels, silt covered more than half the littoral area at low levels and emerging trees shrank (see Roy *et al.,* 2021; and Westrelin *et al.,* 2018 for a detailed description).

The ichtyofauna was dominated by two cyprinids, roach (*Rutilus rutilus*) and common bream (*Abramis brama*), and three percids, ruffe (*Gymnocephalus cernua*), European perch and pikeperch. Northern pike was another common piscivorous species living in the reservoir (Westrelin *et al.,* 2021).

2.2 Species of interest

Northern pike (hereafter named pike) are an ambush predator preferring highly structured areas with vegetation (Chapman & Mackay, 1984; Cook & Bergersen, 1988; Keith *et al.,* 2011): in lakes, they prefer the littoral zone and shallow waters (Craig, 1996; Westrelin *et al.,* 2021), with some versatility observed among sites and sometimes a territorial behaviour (Eklöv, 1992; Skov & Koed, 2004). Pike are mostly active during day or twilight (Baktoft *et al.,* 2012; Beaumont *et al.,* 2005; Cook & Bergersen, 1988; Kobler *et al.,* 2008). Some authors mention seasonal differences with a daytime activity in winter and a twilight activity in summer (Baktoft *et al.,* 2012; Kobler *et al.,* 2008; Říha *et al.,* 2022). In addition, the structural complexity of habitats influences foraging behaviour and activity of pike (Říha *et al.,* 2022).

European perch (hereafter named perch) frequent both littoral zones and neighboring deeper areas in summer depending on the phase of the day (Imbrock *et al.,* 2005; Pekcan-Hekim *et al.,* 2005; Westrelin *et al.,* 2021). They prefer deeper waters in winter (Thorpe, 1977). Young European perch have a group foraging behaviour but large European perch are rather solitary (Craig, 1987; Eklöv, 1992).

Pikeperch prefer deep pelagic areas (Vehanen & Lahti 2003; Westrelin *et al.,* 2021), to seek darkness (Craig, 1987) or prey (Huuskonen *et al.,* 2019). They migrate to deep waters in winter (Říha *et al.,* 2022; Vehanen & Lahti, 2003). Pikeperch are mostly active at dusk (Craig, 2000; Horký *et al.,* 2008).

This knowledge highlights specific feeding strategies, habitat preferences or behaviour of the study species. Within each species, habitat preferences depend on the season (Říha *et al.,* 2022; Westrelin *et al.,* 2021) and the activity shows a diel rhythm (Baktoft *et al.,* 2012; Horký *et al.,* 2008; Jacobsen *et al.,* 2015).

2.3 Tracking data

From March 2012 to March 2014, the three species were tracked by an array of 40 underwater VR2W 69kHz acoustic receivers in the Bariousses reservoir (France). Vemco V9P-2L (47 mm long, 6.3 g in the air) and V8-4L (20.5 mm long, 2 g in the air) acoustic transmitters were used. Specifically, data from 10 Northern pike, 22 European perch and 26 pikeperch (Appendix B) were retrieved to define habitat use and preferences based on their observed positions (Westrelin *et al.,* 2021) and information on the littoral habitat as described in Westrelin *et al*. (2018). Detailed information on the tracking system and the tagging procedure is provided in Roy (2014), Roy *et al.,* (2014) and Westrelin *et al*. (2018).

These tracking data were used to define, for each species, hourly and daily traveled distances, maps of habitat suitability index (HSI) that quantified the attractiveness of each reservoir location according to season and water level, and a density map.

Mean habitat preferences for the three species were quantified by selection ratios of various habitat characteristics: water depth over the whole lake, main substrate type, overhanging vegetation, tree stumps and emerging trees in the littoral zone. They were computed for each season, the season having a strong effect, and for each water level from altitude 507.0 to 513.5 m by 0.1 m. For details on this method, see Westrelin *et al.* (2018). For each species, these selection ratios were aggregated for each combination of season and water level in a HSI index that could be mapped over the lake on a 10 m x 10 m grid (264 maps per species, see Appendix C).

2.4 Model

The *3PLake* model has been developed on the basis of a telemetry dataset with the willingness to use the fewest possible parameterization in order to avoid too much tuning and to facilitate the reproducibility. Only one parameter, the *p* selectivity coefficient, needs to be calibrated. The description of the *3Plake* model below draws heavily from the ODD protocol (Overview, Design concepts, Details), but in a short version fitting to the relative simplicity of our model (Grimm *et al.,* 2010; Grimm *et al.,* 2020).

The *3Plake* model has been developed in Java using SimAquaLife framework (Dumoulin, 2007).

2.4.1 Purpose

The purpose of the *3Plake* model is to simulate individual movements of three fish species (pike, perch, pikeperch) depending on the season and the phase of the day that influence the activity of species depending on their diel cycle and the available habitat (synthesized in an HSI index based on water depth and littoral characteristics of substrate type, overhanging vegetation, tree stumps and emerging trees) (Fig. 1). Its objective is to predict the spatial distribution of fish individuals depending on the habitat availability which is closely linked to the water level. In this case study, the model was calibrated in the Bariousses reservoir.

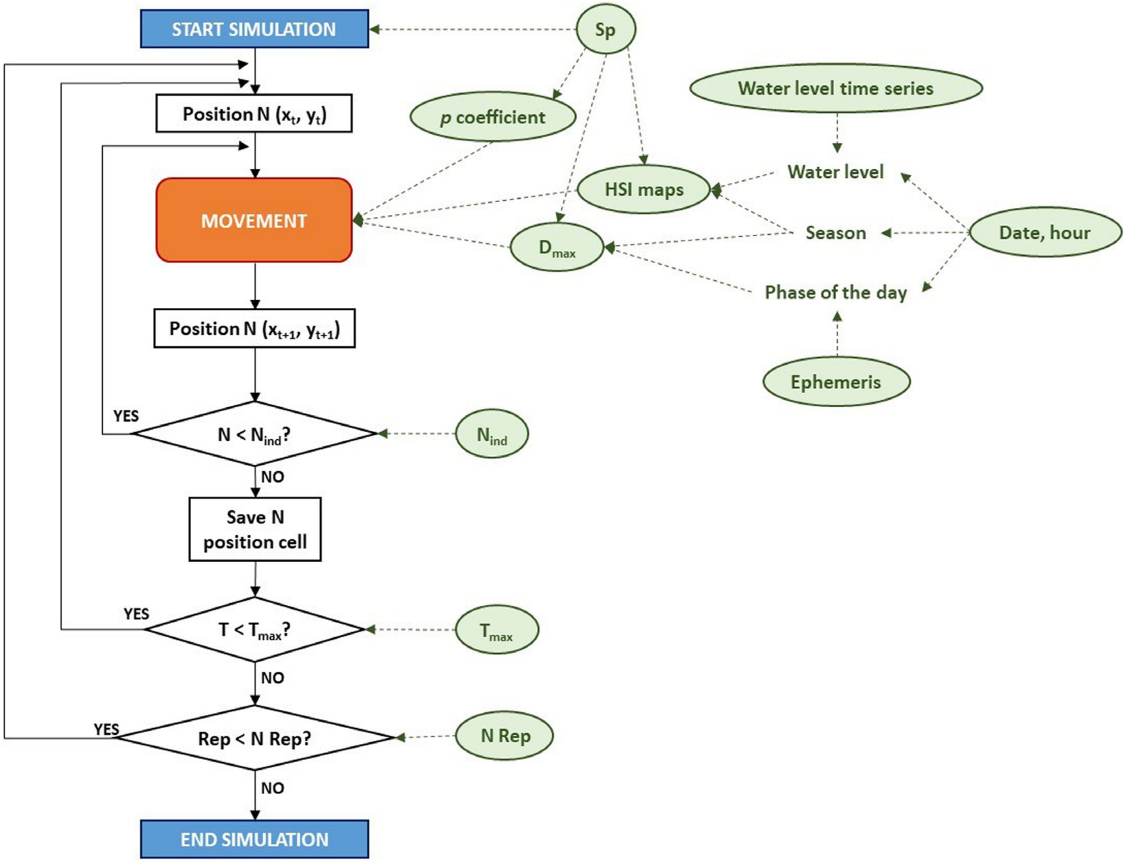


Fig. 1. Flow diagram of processes included in the *3Plake* model. Input data are represented in green ellipses (dotted arrows indicate where they occurred). T_{max} is the number of hourly time steps; D_{max} is the hourly distance range; N_{ind} is the number of individuals in the simulation; N Rep is the number of replicates of the simulation.

2.4.2 Entities, state variables, and scales

The reservoir area was discretized into 10 m x 10 m grid cells.

The entities are the three fish species of interest. Their movements depend on their habitat use and the habitat availability.

The time step is 1 h. The shift between seasons depends on the date: spring (from March 20 to 20 June), summer (from 21 June to 21 September), autumn (from 22 September to 20 December) and winter (from 21 December to 19 March). The phase of the day (dawn, day, dusk, night) changes with the hour according to sunrise/ sunset hours specific to the date. Dawn, that includes the hour preceding the sunrise hour, the sunrise hour itself and the following hour, and dusk, that includes the hour preceding the sunset hour, the sunset hour itself and the following hour, both lasted 3 h.

The model is designed to be applied on an annual cycle. The number of individuals is kept constant in all simulations with no birth and no death.

2.4.3 Process overview and scheduling

One typical realistic year has been built for which at each hour, the season was set from the breakdown exposed in 2.4.2, the phase of the day from sunrise/sunset hours in 2012 and the water level from the time series observed in 2013. For each season combined to each water level and to each species corresponded a HSI map. For each season combined to each phase of the day and each species corresponded an hourly distance range that depends on the level of activity of the species and that defines available cells in which to move in the next hour. HSI maps and hourly distance range, associated with a selectivity coefficient (*p*) (more details in paragraph 2.4.6), drive individual fish movement.

The three species were modeled in independent simulations integrating all individuals from one species.

2.4.4 Design concepts

At each time step, individuals move to a cell which is in the hourly distance range from the previous occupied cell. It depends on the attractiveness of the cell for the chosen species, quantified by the HSI map, and on the *p* selectivity coefficient. The fish movement is assumed to be stochastic among the best available HSI cells. At each time step, the cell in which to move is randomly chosen among a fraction *p* (the selectivity coefficient) of the best HSI cells individual could access, depending on the hourly distance range. Individuals can stay in their initial cell, without moving: it has the same status as other cells, it is only described by its HSI value.

There is no interaction between individuals for perch and pikeperch. To consider the territorial behaviour of pike, two individuals of this species cannot share a same cell.

The position (a cell identifier) of each individual fish is recorded at each time step (a date and an hour).

2.4.5 Initialization

A total of 50 individuals, with similar characteristics to those given in Appendix B, is included in the simulation. This is based on an estimate made from a full draining of the reservoir in

Table I. Input parameters of the 3Plake model and values used in the simulations for the case study.

Name	Description	Value(s) in the simulations
N_{ind}	Number of individuals in the simulation	50
T_{max}	Number of hourly time steps (equivalent to the simulation duration in hours)	8760 (24 h x 365 days), *i.e.*, 1 yr for each simulation
Sp	Species (one species per simulation)	pike, perch and pikeperch
p	Selectivity coefficient: fraction *p* of the cells with the highest HSI within the hourly distance range. The selectivity is high for low values of *p*.	1% and then from 5% to 100% by 5% increment (21 values)
N Rep	Number of replicates of the simulation	10

1997. Initialization is a stochastic process. The starting cell is chosen randomly among all cells.

2.4.6 *Input parameters and input data*

Five input parameters are used in the *3Plake* model (Tab. I).

The *p* coefficient is the only parameter used to calibrate the model. The calibration procedure is detailed in the Model evaluation paragraph (2.4.8.).

In addition, the *3Plake* model needs four input data:

- The *ephemeris* of the year to access to the sunrise and the sunset hours to define the phases of the day;
- The *hourly water level time series* (see Appendix A for this case study);
- The *HSI map* for each species and for each combination season*water level (264 maps per species) (see Appendix C for this case study);
- The *hourly distance range* (D_{max}) that defines the maximum distance between two consecutive positions of an individual in the model. It was calculated using the telemetry dataset. For each species, there is one value for each combination season*-phase of the day (16 values per species) (Appendix D for this case study). This hourly distance range is set as the mean hourly distance estimated over data multiplied by 1.7. This value was chosen (i) to simulate mean hourly distances that approached the empirical values and (ii) to get 80% of the observed hourly distances smaller than D_{max} for all combinations of season*-phase of the day.

2.4.7 *Submodels*

Environment and species characteristics are updated at each time step:

- The date and the hour define the current season and phase of the day;
- The water level changes following the hourly water level time series;
- The species HSI map changes depending on the season and the water level;
- The species D_{max} is updated according to the season and phase of the day.

At each time step, individuals move to a cell within D_{max} range from the previous position and which is in the lake at the water level corresponding to the time step. The candidate cells depend on their attractiveness, quantified by their HSI value, and on the *p* selectivity coefficient of the simulation. A lower value of *p* corresponds to a more selective habitat choice (towards higher quality). A higher value of *p* corresponds to a less selective habitat choice; a value of 100% for *p* means that the habitat choice is random among the accessible cells.

We ran 10 replicates for each value of *p*, giving a total of 210 simulations per species (Tab. I). All simulations were run with 50 individuals and the time period covered lasted one year.

We calculated the following metrics with simulation outputs:

- The hourly traveled distance, which is the Euclidean distance between two consecutively occupied cells.
- The daily traveled distance, which is the Euclidean distance between the cell of an individual at the first hour of a calendar day and the cell of the same individual 24 h later. The daily distance measures the net effect of the prospecting behaviour at a daily scale.
- The species density map, which is the total number of positions (from all individuals of the considered species) recorded in each cell over all time steps of a simulation.

2.4.8 *Model evaluation*

The traveled distance metrics were used to evaluate the range of suitable *p* values for each species. The objective of the *3Plake* model was to simulate the spatial distribution of each species. Therefore, the comparison between simulated and observed density maps was used for the final calibration of *p* for each species.

Hourly distance

Yearly mean hourly distance

For hourly distances, the evaluation of the simulations was first based on a comparison of the simulated means by species (mean and range across the 10 replicates for each value of *p*) with the observed means.

Because of non-continuous observed data, the observed hourly distance was calculated as the Euclidean distance between the first position of an hour and the first position of the next hour when the time lag separating these positions was between half an hour and one hour and a half. We assigned a zero value to all distances smaller or equal to 3 m, which was the telemetry system mean position error (Roy *et al.,* 2014).

For a fair comparison of the simulations with the observations, the yearly mean observed hourly distance was defined as the mean of the four seasonal means to equally weigh the season. Then we calculated a 95% confidence interval for this observed mean using bootstrap (1,000 resamplings with replacement; the 95% confidence interval is thus given by the 25th and 975th values sorted in increasing order).

For each species we identified an optimal value of *p* simulating the least biased mean hourly distance, *i.e.*, the value for which the mean of simulated hourly distances was the closest to the observed one (Westrelin *et al*., 2021). We also calculated 1,000 bootstrap values of the difference between the observed and simulated yearly mean hourly distances (resampling the individuals for the observed means, and sampling randomly one of the 10 replicates for the simulated means). The percentiles 2.5 and 97.5 of these 1,000 values defined a 95% confidence interval of this difference. The difference between the observed and simulated yearly mean hourly distances was significant when this 95% confidence interval did not include zero.

Hourly distance distribution

Then, for each species, we used boxplots to compare the distribution of simulated hourly distances for each value of *p* with that of observed ones.

For each species and each value of *p*, we built a boxplot with 40,000 simulated hourly distances that were randomly chosen out of all simulated replicates and time steps.

Additionally, we built a boxplot of observed hourly distances for each species. To equally weigh each season similarly to the simulations, we sampled 10,000 values with replacement for each of the four seasons, and we used these 40,000 values to build the boxplot.

Daily distance

We calculated the observed daily distance with a duration separating both positions comprised between half a day and a day and a half, because of non-continuous observed data. We applied the same principles as for the hourly distances to compare simulated and observed daily distances.

Density map

For the observed density map, we first calculated a density map for each season, for which the density in a cell was the total number of positions recorded in this cell (corrected by the probability of positioning in this cell by the telemetry system, see Roy *et al*. (2014) for this probability map). Then, we calculated the yearly map as the cell-by-cell weighed mean of the four seasonal maps. The weights were the inverse of the total number of recorded positions in the season to give each season the same weight. See Appendix E.

Next, we centered and standardized the simulated and observed density maps considering only cells with a non-null probability of positioning by the telemetry system (Roy *et al.*, 2014). Then, for each cell, we computed the square differences of simulated and observed centered and standardized densities and summed them over all cells of the map. The Euclidean distance was the square root of this sum. Thus, for each species and each *p,* we obtained a mean and a range of this distance based on the 10 replicates. We also calculated a randomized model of this distance by randomizing the cell positions in the simulated density map before calculating its distance to the observed one (the used replicate of the simulation was randomly chosen each time). We repeated this randomization 1,000 times to calculate a mean and a 95% confidence interval. This bootstrap on the null model allowed to identify when the simulated distribution was closer to the observed distribution than would be a randomized distribution, in other words when the *3Plake* model was more informative than the null model.

For each species, we identified the value of *p* and its 95% confidence interval for this density map distance using bootstrap. For each value of p, we randomly sampled one value of the distance between density maps among the 10 replicates. Then we identified the value of p which led to the minimum distance for this sample. We repeated this 1,000 times to get 1,000 values for p. For each species, the best value of p was the mean across these 1,000 bootstrap values, and the 95% confidence interval was defined by the percentiles 2.5 and 97.5.

Finally, in addition to the density map distance, we mapped the differences between simulated and observed centered and standardized densities for the optimal p value of each species to spatially identify them.

3 Results

3.1 Hourly distance

Yearly mean of simulated hourly distances increased with the selectivity parameter p. The three species presented the same general pattern: a steep rise for small values of p (up to 5–10%) and then a slight linear increase (Fig. 2 and Appendix F Fig. F1). The simulated distances were very close between the ten replicates (amplitude less than 1 m). But there was a larger uncertainty in the yearly mean of observed hourly distances (*i.e.*, a large confidence interval; Fig. 2). Hence, the mean of simulated distances was not significantly different from the mean of observed distances for a large range of values of p. The numerical values obtained by bootstrap for the p values giving unbiased estimate of this yearly mean were $p = 70\%$ (range 10–100%) for pike, $p = 60\%$ (range 20–100%) for perch and $p = 30\%$ (range 10–100%) for pikeperch (Tab. II).

The distribution of simulated hourly distances was less dispersed than that of the observed ones whatever the value of p in this range for all species (Fig. 2 and Appendix F Fig. F1). Specifically, simulations captured fewer short distances (null distances in the observations) and could not get the largest ones.

3.2 Daily distance

The yearly mean of simulated daily distances increased with p for all species. For a given p value, replicates gave very close distances (Fig. 3 and Appendix F Fig. 2). But there was a larger uncertainty in the observed yearly mean of daily distances. The mean of simulated distances was not significantly different from the mean of observed distances for a large range of p values. By bootstrapping, the optimal p values were $p = 70\%$ (range 10–100%) for pike, $p = 20\%$ (range 10–65%) for perch and $p = 95\%$ (range 50–100%) for pikeperch (Tab. II). In general, there was a large overlap of p value ranges between hourly and daily distances (Tab. II).

Similarly to the hourly distance, the distribution of simulated daily distances was less dispersed than that of the observed ones whatever the p value (Fig. 3 and Appendix F Fig. F2).

3.3 Distance between simulated and observed density maps

The distance to observed density maps was generally smaller for the *3Plake* model simulations than for the null model (Fig. 4 and Appendix F

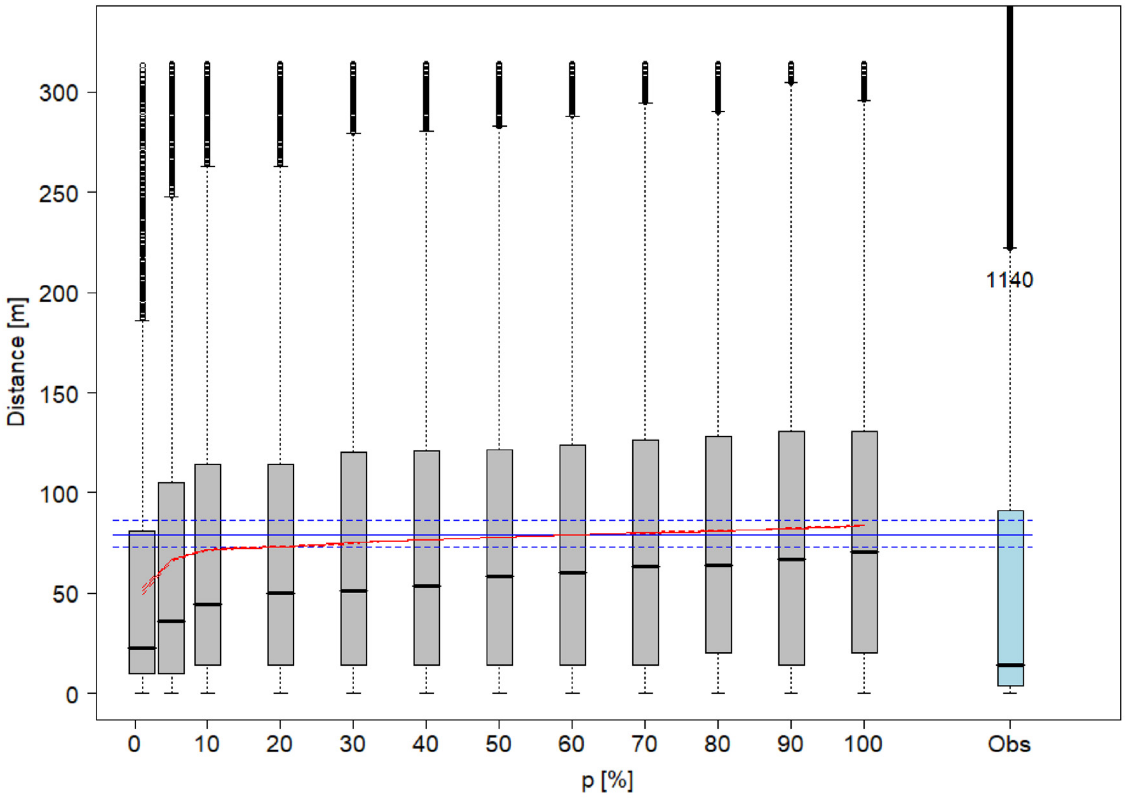


Fig. 2. Yearly mean of simulated hourly distances for perch as a function of the selectivity parameter, *p*, varying from 1% to 100%. The solid red line represents the simulated mean (across all time steps, all individuals and all replicates) and the dashed red lines its range over the ten replicates (very close to the mean). The solid blue line is the yearly mean of observed hourly distances over all data and the dashed blue lines are its 95% confidence interval. Each grey boxplot represents the simulated distribution of the hourly distances for the 365 × 50 × 10 × 24 h. The blue boxplot stands for observed values. The extreme values of the observed boxplot are truncated and the maximum value, 1140, is displayed. Boxplots represent extreme values and 25%, 50% and 75% quantiles.

Table II. Parameter p (optimal value and range obtained by bootstrap) for which simulation and observation minimized the chosen metrics for each of the following criteria: mean hourly distance, mean daily distance and distance between density maps.

	Pike	Perch	Pikeperch
Hourly distance	70% (10–100%)	60% (20–100%)	30% (10–100%)
Daily distance	70% (10–100%)	20% (10–65%)	95% (50–100%)
Density map	10% (10–10%)	20% (5–50%)	61% (25–90%)

Fig. F3), except when $p>60\%$ for pike. Based on the bootstrap, the optimal *p* values (minimizing the distance between observed and simulated maps) depended on the species: a smaller value for the pike (10%, range 10–10%), an intermediate value for the perch (20%, range 5–50%) and a higher value for the pikeperch (61%, range 25–90%) (Tab. II). The graphic visualization based on the mean over the 10 replicates (Fig. 4) can differ from the numerical results given by the bootstrap (Tab. II). So, pike seemed to have a spatial distribution linked to quite a high selectivity (low *p*) whereas pikeperch seemed to have a weaker selectivity with respect to HSI. Importantly, the best value identified for *p* for the density map criteria was in the range of the ones identified for hourly and daily distances (Tab. II). In other words, for the best *p* value identified for the density criteria, the yearly means of both hourly and daily distances did not differ significantly from the observed ones.

3.4 Density maps

Differences between simulated and observed density maps were displayed for each species, for the optimal value of the *p* selectivity coefficient (Fig. 5). For the three species, some specific areas of the reservoir revealed higher simulated densities compared to observations. These areas were located mostly in the upstream half of the lake for perch (Fig. 5b) and pikeperch (Fig. 5c), whereas lower densities (compared to observations) were simulated in the downstream part of the lake, especially for perch (Fig. 5b). However, for pike (Fig. 5a) those areas of higher simulated densities (compared to observed ones) were situated in narrow littoral portions both upstream and downstream. Observed density maps are displayed in Appendix E.

4 Discussion

4.1 Input data

The *3Plake* model needs few and easy to get input data, apart from the HSI maps. In addition, HSI maps are key drivers of this model that assumes that fish movements are mainly driven by the habitat use. Telemetry data are very suitable to compute HSI maps, but they could also be calculated from physical data coupled with available habitat preference models (Laura *et al.,* 2020; Rosenfeld, 2017).

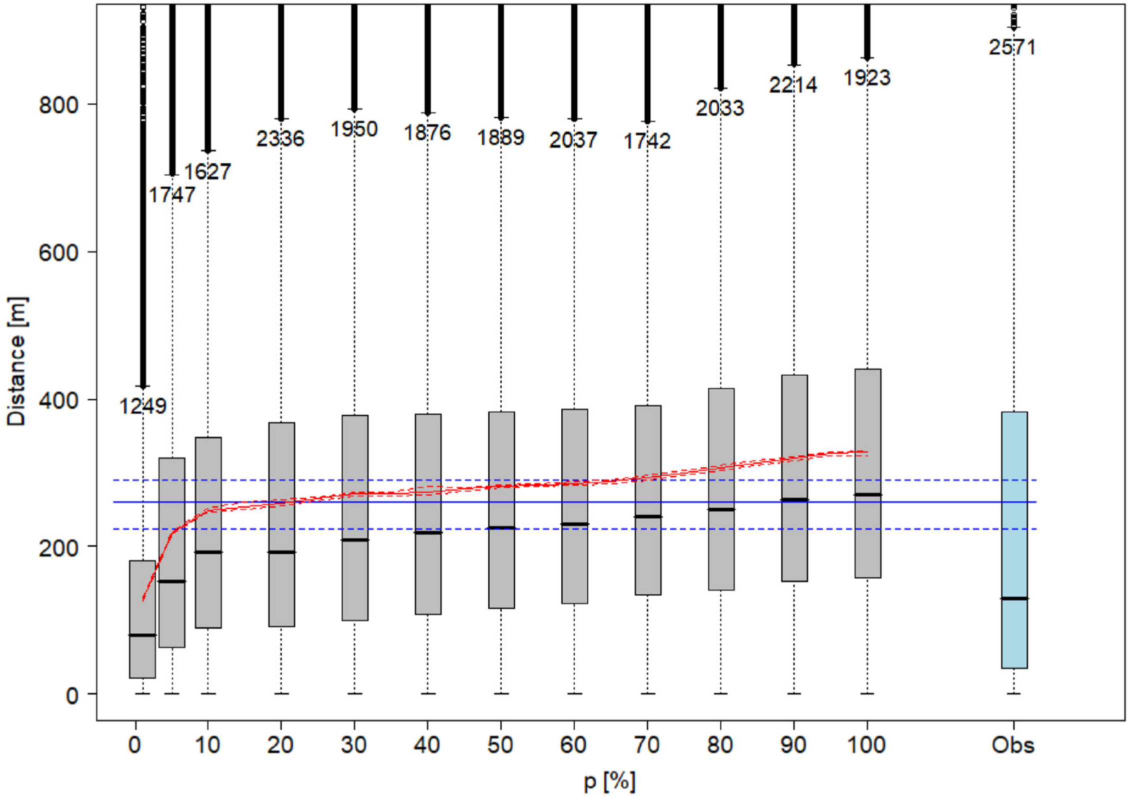


Fig. 3. Yearly mean of simulated daily distances for perch as a function of the values of p varying from 1% to 100%. The solid red line is the simulated mean (across all time steps, all individuals and all replicates) and the dashed red lines its range over the ten replicates (very close to the mean). The solid blue line is the yearly mean of observed daily distances over all data for Perch, and the dashed blue lines its 95% confidence interval. Each grey boxplot represents the simulated distribution of the daily distances of the $365 \times 50 \times 10$ days. The blue boxplot stands for observed values. The extreme values of the boxplots are truncated and the maximum value is displayed on each boxplot. Boxplots represent extreme values and 25%, 50% and 75% quantiles.

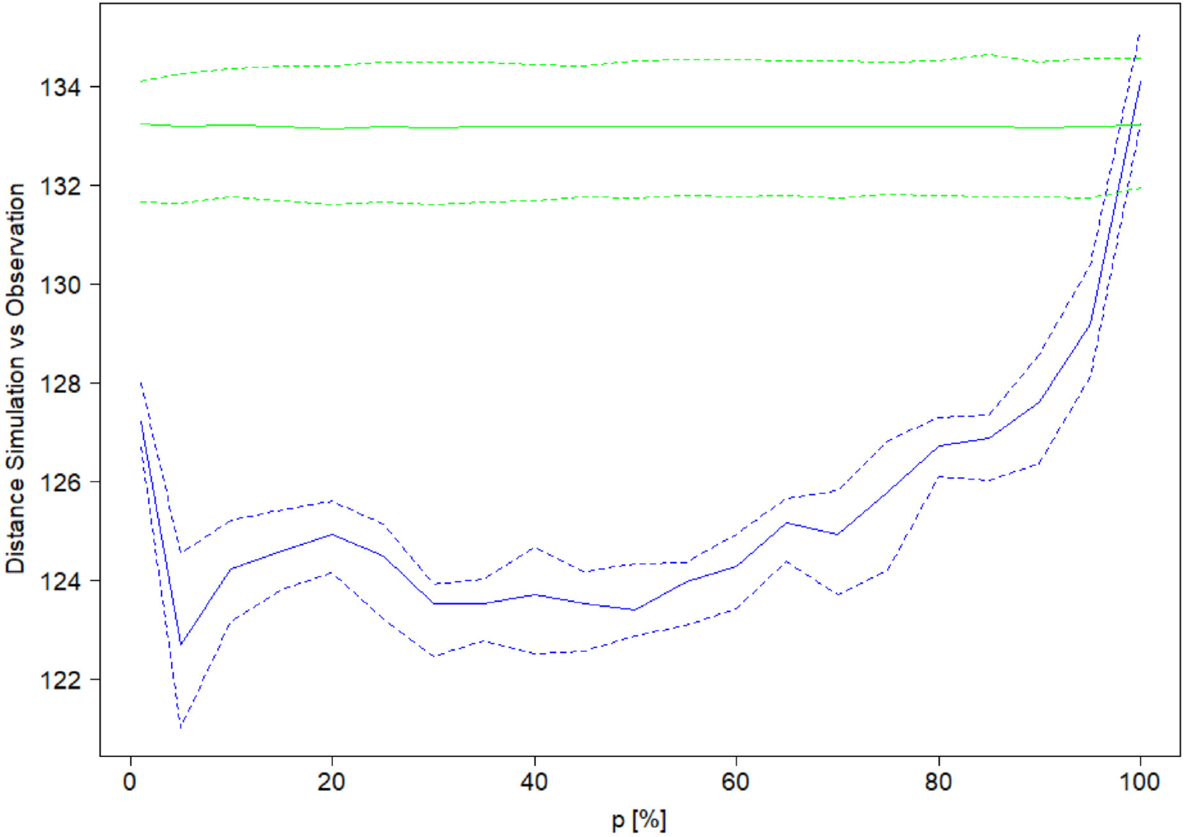
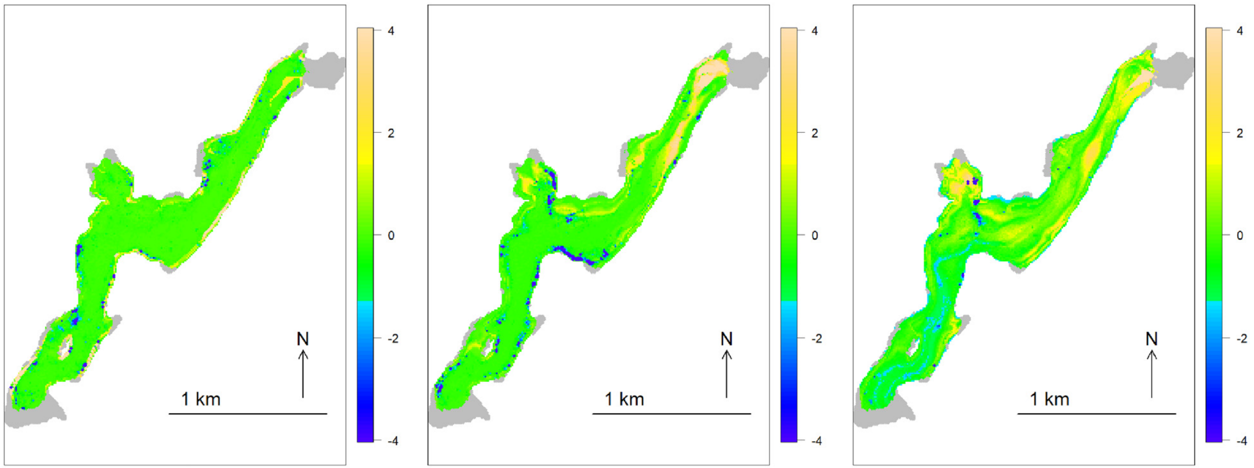


Fig. 4. Distance between simulated and observed densities for perch as a function of *p*. The solid blue line is the mean over the 10 replicates and the dashed blue lines the range over the 10 replicates. The null model of this distance is also represented (mean over 1,000 repetitions and 95% confidence interval corresponding to the 2.5 and 97.5 quantiles of these 1,000 values, respectively in green solid line and dashed green lines).



(a) (b) (c)

Fig. 5. Difference between simulated and observed density maps (unitless) for the optimal *p* value for each species, (a) pike ($p = 10\%$), (b) perch ($p = 20\%$) and (c) pikeperch ($p = 61\%$). Positive values indicate larger density values for simulation than for observation. Negative values indicate smaller density values for simulation than for observation. Values smaller than -4 and larger than 4 are truncated to -4 and 4 on the map. Grey color indicates blind areas where no fish could be tracked by the telemetry system. Upstream part is to the North-East and downstream part to the South-West.

4.2 Calibration of the *3Plake* model

The calibration of the *3Plake* model is only based on the *p* selectivity coefficient (fraction *p* of the cells with the highest HSI within the hourly distance range). The traveled distance metrics were used to evaluate the range of *p* values whereas, in the end, the density maps were used to choose the *p* value for each species. In the Bariousses reservoir and for each of the three species, the best *p* value evaluated by density maps matched with the range of *p* values according to hourly and daily distances. They were quite different between species with $p = 10\%$ for pike, $p = 20\%$ for perch and $p = 61\%$ for pikeperch. This illustrates that the three fish species showed different degrees of habitat selectivity (higher habitat selectivity for lower *p* values). For pike and perch, the values of *p* that led to the best match between simulated and observed density maps were lower than for pikeperch. This was in agreement with the higher habitat selectivity of pike and perch than pikeperch. It was particularly the case for pike ($p = 10\%$, a value given by all 1,000 bootstrap iterations), a species that is known for being strongly attracted to highly structured habitats with vegetation and shallow waters (Inskip, 1982; Kobler *et al.,* 2008). Perch revealed a slightly lower habitat selectivity ($p = 20\%$, with a larger range of 5–50). Indeed, even if the species was attracted by littoral and near-littoral areas (Westrelin *et al.,* 2018), it could use the pelagic zone (Jacobsen *et al.,* 2015; Westrelin *et al.,* 2021) and showed a more plastic behaviour (Craig, 2000). Furthermore, it was shown to adapt its habitat use to minimize interactions with other competitors as pike or pikeperch (Schulze *et al.,* 2006). Pikeperch was the species with the lowest habitat selectivity ($p = 61\%$) and with the largest confidence interval for *p* (25–90). Pikeperch frequents deeper waters (Craig, 1987) and the pelagic zone (Vehanen & Lahti, 2003) but can also be found in shallower waters depending on the season (Vehanen & Lahti, 2003; Westrelin *et al.,* 2021). The density maps observed in the Bariousses reservoir confirmed the larger spectrum of habitats used by pikeperch (Appendix E, Fig. E1). Indeed, this species is known to live in a large range of aquatic ecosystems, including those widely anthropized (Kangur *et al.,* 2007; Poulet *et al.,* 2005).

The various degrees of habitat selectivity of species highlight their adaptability to their environment. Pike seemed to be the most specialist species, with the lowest *p* value and *p* value range. As a result, this species is potentially more vulnerable to pressure than perch or pikeperch. Indeed, throughout its native distribution area, in some cases, stocking supports pike populations to compensate environmental degradation (Guillerault *et al.,* 2021; Pierce, 2012). As the reproductive success of pike is very dependent on littoral habitats, the species is particularly vulnerable in reservoirs subject to water level fluctuations (Casselman & Lewis 1996; Crane *et al.,* 2015; Hudon *et al.,* 2010); it can also be impacted by invasive species (Rehage *et al.,* 2016). In contrast, pikeperch revealed a low habitat selectivity (higher *p* value), coherent with its recent increasing abundance in lakes and reservoirs (Huuskonen *et al.,* 2019; Jeppesen *et al.,* 2012) also linked to beneficial effects of climate change on this species (Pekcan-Hekim *et al.,* 2005).

4.3 Gaps between observations and simulations

We observed some gaps between observations and simulations on evaluation metrics: the *3Plake* model (i) did not represent the longest observed hourly distances, (ii) underestimated the motionless behaviour and (iii) slightly diverged from the observed density map in certain areas depending on species.

Hourly simulated distances were limited by maximum values (D_{max}) that hindered the model from simulating the longest observed hourly distances. However, these maximum values were chosen to control the mean distance, and so, to relax this constraint by increasing these maxima would have led to an overestimation of the mean simulated distance compared to the observation. Daily distances were less impacted by this constraint and observed and simulated daily patterns were more in agreement than hourly ones. Even if daily distance is not defined as the numerical addition of 24-hourly segments, it takes into account these 24 simulated hourly movements which could help to simulate daily movements at longer distances, closer to the observed longer daily distances.

Motionless behaviours were also less often simulated than observed, especially in the hourly movements. Independent of HSI, since the probability to move to a cell was the same for all cells within the maximum distance range, the probability to simulate immobility (fish that stays at the same position) was low compared to the observations. Actually, in the input data, neither HSI nor maximum distance range are informative on this motionless behaviour. To capture this feature could be a further improvement of the model.

The *3Plake* model tended to slightly overestimate the densities in the upstream part and some narrow littoral areas of the reservoir at the expense of the downstream part. Except for perch, the highest densities simulated towards the main tributary were in agreement with numerous studies based on observations (*e.g.*, Brosse, 1999; Prchalová *et al.,* 2009; Prchalová *et al.,* 2008; Świerzowski *et al.,* 2000; Vašek *et al.,* 2016), in relation with the riverine origin of the fish fauna and the presence of an upstream-downstream productivity gradient (Vašek *et al.,* 2006). The comparison between observed and simulated density maps (visually and with the Euclidean distance) could have been limited by the fact that, for each species, observed maps were built on a subsample of the species population. The subsamples could have been too small, at least in some seasons, to be representative. This could be enhanced in species showing territorial behaviour as pike (Eklöv, 1992; Skov & Koed, 2004), which moreover had the lowest sample size of ten individuals throughout the whole study, and artificially led to null density zones in the observed map. On the other hand, this could illustrate the complementarity of simulations and observations: by extracting habitat preferences from a set of individuals and then applying them to a representative sample of the population, the model is able to catch, or at least to give insight into, features that could not be handled with few observations.

4.4 Perspectives

The *3Plake* model represents quite well the spatial distribution of three fish species in the Bariousses reservoir. However, the model has been designed to be applied on an annual scale and, as such, is not appropriate to focus on the movements during the spawning period, which constitutes a zoom on a particular period. Now, a process of spatial search and selection of spawning habitat could be added to the model and activated in the species adequate periods (Baetens *et al.,* 2013; Clark *et al.,* 1998; Clark *et al.,* 2008). Such a model could be used to predict the effects of habitat restoration or water level scenarios on the spawning success of the three fish species. Similarly to spawning habitat, habitat restoration would lead to new HSI maps that could be built with fish habitat preferences already available in the reservoir. Comparing model outputs from simulations based on these restored maps with simulations run with non-restored ones would give insights into theoretical impacts of the restoration on spawning success. The same approach could be applied to compare different WLF scenarios.

5 Conclusions

The *3Plake* model, calibrated using high resolution data, is only based on HSI maps and maximum hourly distances. Though quite simple, it simulated some interesting patterns of movement and habitat selection as discussed above. It is generic and could be applied to many other fish species as long as HSI maps and hourly distance range are available at each time step. It implicitly integrates some biotic interactions among individuals or among fish species, because model inputs are based on high resolution observations when all three species coexisted in the reservoir. Other biotic factors, such as prey distribution in the reservoir, are also implicitly partly integrated into HSI maps, because in relation with physical habitat.

The *3Plake* spatially explicit IBM simulated yearly mean hourly and daily distances for pike, perch and pikeperch. Specific values of the selectivity parameter made it possible to simulate fish spatial densities close enough to the observed ones to be informative and consistent with the available habitat. A next step will be the addition of a spawning module to predict the impact of habitat restoration or water level management on the population dynamics. This final model could be a useful tool for stakeholders, to get insights into the effects of environmental measures on fish densities and fish spawning success.

Table B.1 Mean (range) of tracking days, number of positions, total length and weight are given over the pool of individuals by species.

Species	**Number of individuals**	**Number of tracking days**	**Number of recorded positions per individual**	**Total length (mm)**	**Weight (g)**
Pike	10	122 (8-420)	15759 (128-55394)	532 (425-629)	958 (398-1513)
Perch	22	182 (16-442)	38245 (2392-117621)	402 (320-486)	956 (383-1800)
Pikeperch	26	126 (5-442)	31102 (818-125551)	494 (360-695)	1136 (354-3000)

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Supplementary material

An individual-based model to predict the spatial distribution of northern pike, European perch and pikeperch from habitat use in a reservoir subject to water level fluctuations Un modèle individu-centré pour prédire la distribution spatiale du brochet, de la perche commune et du sandre, à partir de l'utilisation de l'habitat dans un réservoir soumis à des fluctuations de niveau d'eau

Appendix A: Water level fluctuation

Figure A1. Water level time series over the tracking period (March 2012 - March 2014). Data are hourly and their vertical resolution is 0.1 m. The horizontal red arrow indicates the yearly time series used for the simulation: year 2013.

Appendix B: Characteristics of tracked individuals of pike, perch and pikeperch

Appendix C: HSI calculation

For each of the three species, a selection ratio (SR) was calculated for five habitat variables, independently for each season, following the method of Westrelin et al. (2018) for perch. The first variable was water depth (divided in 7 depth classes for SR calculation: [0; 2.5[, [2.5; 5[, [5; 7.5[, [7.5; 10[, [10; 12.5[, [12.5;15[, [15; 22[m). It was available for the whole lake and was updated at each time step with the water level time series. The four other variables were main substrate (silt, sand, gravel, pebble, stone, boulder, rock and lawn which made a particular class as no other vegetation was observed except these flooded lawns), overhanging vegetation (yes, no), tree stumps (yes, no) and emerging trees (yes, no) in the littoral zone. These last ones were only available in the littoral zone.

Table D.1 Maximum hourly distance (Ra in m) for each species, season and phase of the day

		Phase of the day			
Species	Season	Dawn	Day	Dusk	Night
Pike	Spring	204	233	199	53
	Summer	153	201	94	31
	Autumn	151	131	117	29
	Winter	172	133	170	78
Perch	Spring	177	175	99	15
	Summer	235	308	156	27
	Autumn	170	248	117	15
	Winter	128	148	105	10
Pikeperch	Spring	60	36	58	53
	Summer	206	92	184	170
	Autumn	134	56	148	136
	Winter	126	44	94	77

The habitat suitability index (HSI) was calculated for each 10 m x 10 m cell and each time step as the sum of the local SR for each variable divided by the sum of the maximum SR for each variable. For the littoral area, the HSI was calculated with the five variables. For the center of the lake, the HSI was calculated with the water depth variable only.

In order to have a synthetic visual representation of HSI data, the HSI was averaged over the year (Figure C1) and in each season (Figure C2 for pike, Figure B3 for perch and Figure C4 for pikeperch) with the water level time series used for simulations.

Figure C1. HSI map (averaged along the year with the water level time series used for simulations) for (a) pike; (b) perch; (c) pikeperch. Color legend: from white, low HSI, to red, high HSI.

Figure C2. HSI map (averaged along the days of a season with the water level time series used for simulations) for pike during (a) spring, (b) summer, (c) autumn, (d) winter. Color legend: from white, low HSI, to red, high HSI.

Figure C3. HSI map (averaged along the days of a season with the water level time series used for simulations) for perch during (a) spring, (b) summer, (c) autumn, (d) winter. Color legend: from white, low HSI, to red, high HSI.

Figure C4. HSI map (averaged along the days of a season with the water level time series used for simulations) for pikeperch during (a) spring, (b) summer, (c) autumn, (d) winter. Color legend: from white, low HSI, to red, high HSI.

Appendix D: Hourly distance range

Appendix E: Observed fish density map

Figure E1. Observed density map for (a) pike, (b) perch and (c) pikeperch. Color legend: from white, low densities, to red, high densities. The log of the mean yearly density is represented. The grey areas are blind areas where no fish could be detected by the tracking system.

Appendix F: Supplementary figures

Figure F1. Mean simulated hourly distance for (a) pike and (b) pikeperch over a year as a function of p parameter varying from 1 to 100 %. The solid red line is the simulated mean (across all time steps, all individuals and all replicates) and the dashed ones are its range over the ten replicates (very close to the mean). The solid blue line is the mean observed hourly distance over all data and the dashed ones are its 95% confidence interval. Each grey boxplot represents the simulated distribution of the hourly distances for the 365x50x10x24 hours. The blue boxplot stands for observed values. The extreme values of the observed boxplot are truncated and the maximum value is displayed.

Figure F2. Mean simulated daily distance for (a) pike and (b) pikeperch as a function of the values of p varying from 1 to 100 %. The solid red line is the simulated mean (across all time steps, all individuals and all replicates) and the dashed ones its range over the ten replicates. The solid blue line is the mean observed daily distance over all data for each species, and the dashed ones its 95% confidence interval. Each grey boxplot represents the simulated distribution of the daily distances of the 365x50x10 days. The blue boxplot stands for observed values. The extreme values of the boxplots are truncated and the maximum value is displayed on each boxplot.

Figure F3. Distance between simulated and observed densities (mean and range) for (a) pike and (b) pikeperch as a function of p. The solid blue line is the average over the 10 replicates and the dashed blue lines are the range over the 10 replicates. The null model of this distance is also represented (mean and 95% confidence interval over 1,000 repetitions, respectively in green solid line and dashed green lines).

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